

LATE CRETACEOUS GYMNOSPERMS FROM SAKHALIN AND THE TERMINAL CRETACEOUS EVENT

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ABSTRACT. In the Late Cretaceous, diversity of gymnospermous orders increased due to the appearance of true Cycadales. Most groups experienced important evolutionary changes. Extant genera first appeared among Cycadales (*Cycas*), Ginkgoales, and Coniferales. Noteworthy evolutionary innovations were phylloclades in the Cupressaceae and distinctive stomatal types in the Araucariaceae. *Sequoia* and *Parataxodium* achieved dominant status. At the Cretaceous Tertiary boundary, the Caytoniales, Bennettitales, and Nilssoniales died out. There was replacement of dominant genera among conifers and of dominant leaf morphotypes among angiosperms. Major type of the Late Cretaceous vegetation—*Sequoia*-laurophyllous forest—perished and gave way to mixed broad-leaved forests.

PALAEOBOTANICAL studies of the Late Cretaceous have traditionally centred on angiosperms while gymnosperms of this age have been practically neglected. It was assumed that in the Late Cretaceous the era of gymnosperms was over, their evolutionary potentials were nearly exhausted, and their history was that of gradual retreat before prospering angiosperms. This notion led to serious misunderstanding of the Late Cretaceous vegetation and, consequently, of the events at the Cretaceous-Tertiary (K-T) boundary. In the present study of the Late Cretaceous flora of Sakhalin which is the classical Asiatic flora of this age, equal attention was paid to angiosperms, gymnosperms, and other groups. The validity of such generic designations as *Dryophyllum*, *Quercus*, *Populus*, *Vitis*, *Ilex*, *Zizyphus*, *Ficus*, *Crataegus*, *Viburnum* (Kryshtofovich and Baikovskaja 1960) was questioned and the list of Senonian angiosperms considerably reduced. Several species of *Sequoia* described by Kryshtofovich and Baikovskaja may belong in no more than one species, but generally the gymnosperms are represented by well-defined species. Full descriptions will be given in a monograph on the Cretaceous flora of Sakhalin. The most essential results bearing on the taxonomy and evolutionary history of gymnosperms are summarized in this paper.

STRATIGRAPHY

The plant-bearing beds of western Sakhalin range from Coniacian to Miocene in age, using evidence from marine invertebrates. The Senonian sequence consists of deltaic cyclothems and flyshoid turbidites assigned to several formations. Four successive floristic horizons are recognized. They correspond to the faunistic zones of (1) *Inoceramus uwajimensis* (Coniacian), (2) *Anapachydiscus naumanni* (Santonian or early Campanian), (3) *I. orientalis* (early Campanian), and (4) *Pachydiscus subcompressus* (late Maastrichtian). The *I. schmidti* beds between (3) and (4) contain sparse plant fossils. The uppermost Maastrichtian beds are overlain by tuffaceous

strata (the Boshniakovian Formation) which yielded a plant assemblage much different from Senonian flora, though containing occasional *Cladophlebis frigida* and *Nilssonia*. The Boshniakovian Formation grades laterally into marine beds with an impoverished fauna of small bivalves of Danian aspect. Above them there are conglomerates and shales with Palaeogene plants.

The major plant localities are:

Mgachi near Alexandrovsk City, Santonian. This locality had yielded the first Asiatic fossil plants of Cretaceous age, described by Oswald Heer in 1878. Most of the structurally preserved material came from this locality.

Cape Jonquier at Alexandrovsk City, early Campanian, a locality famous for its marine invertebrates. Plants came from several thin layers intercalated in the shell beds.

Augustovka River, near the village Boshniakovo, Maastrichtian and Danian. Plant material was found in the paralic beds of late Maastrichtian age and above them in tuffaceous strata assigned to the Danian. Plants are abundant, but mostly without cuticles.

Forty minor localities scattered along the western coast of Sakhalin have also been studied; they provided material for palaeoecological studies.

The collections are in the Institute of Biology and Pedology, under NN 301 to 340.

GYMNOSPERMS

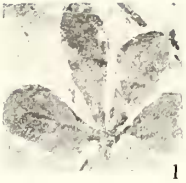
The Senonian flora shows no reduction in the diversity of higher gymnosperm taxa relative to the Jurassic or Early Cretaceous floras. At least seven orders of gymnosperms—the Caytoniales, Nilssoniales, Bennettitales, Ginkgoales, Czekanowskiales, Cycadales, and Coniferales occur in Senonian localities.

Caytoniales

Sagenopteris from Mgachi is much like *S. colpodes* Harris (Yorkshire Jurassic) showing upper epidermis cells with sinuous walls. However, the leaves are smaller, there are numerous hairs in the costal zones, and the cuticle of subsidiary cells extends below the guard cell thickenings (Pl. 103, fig. 2) while in the Jurassic species they are in one plane (Harris 1964). Relative to a time span of about 100 my these differences are rather small. The Caytoniales display remarkable evolutionary conservatism.

EXPLANATION OF PLATE 103

- Figs. 1, 2. *Sagenopteris* from the Senonian of Sakhalin, Mgachi. 1, leaf, 308-592, $\times 2$. 2, stoma, inside view, the cuticle of subsidiary cells is extending under the guard cell thickenings, 308-496, SEM, $\times 2000$.
 Fig. 3. Ginkgoalean seed, same locality, 308-641, $\times 1.5$.
 Figs. 4-7. *Nilssonia serotina* Heer, same locality. 4, 'Nilssonia bed', crowded entire leaves, 313-265, $\times 1$.
 5, segmented leaf, 306-66, $\times 1$. 6, stoma, 306-593, SEM, $\times 2200$. 7, ribbed cell walls, 306-593, SEM, $\times 850$.
 Fig. 8. Ginkgoalean leaf cuticle, stoma, same locality, 304-10, SEM, $\times 1500$.
 Fig. 9. *Pterophyllum* from the uppermost Maastrichtian, Augustovka River, 329-364, $\times 1$.



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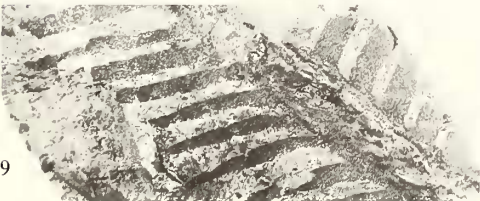
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Nilssoniales

The late Cretaceous *Nilssonia serotina* Heer has both entire and segmented leaves. This type of leaf polymorphism is recognized in some early Mesozoic species, such as *N. polymorpha*. Surprisingly, it is virtually unknown in the Early Cretaceous species. The cuticle is typical nilssonialean, with strongly ribbed cell walls. The bulging cells are often laterally compressed. The guard cells of *Nilssonia* are usually indistinct when viewed under the light microscope, but in the SEM they can be seen to form a keyhole-shaped stoma (Pl. 103, fig. 3).

Bennettitales

Pterophyllum leaves occur in the uppermost Senonian just below the tuffaceous Boshniakovian beds. They are preserved as incrustations without cuticles (Pl. 103, fig. 8).

Ginkgoales

The ginkgoalean seeds from the Senonian localities are more like those of the extant *Ginkgo* and much larger than their Jurassic and Early Cretaceous predecessors (up to 17 mm long, while in the latter 10 mm is the upper limit) which means also less ovules per ovuliferous organ. The leaves are of *G. biloba* type, with sparse hairs and less protected stomata than in the geologically older species (Pl. 103, fig. 7). One can surmise that true *Ginkgo* first appeared in the Late Cretaceous, later than some extant angiosperm genera. The great antiquity of *Ginkgo* assumed in the cytochrome c trees and some other phylogenetic reconstructions is not supported by the geological record.

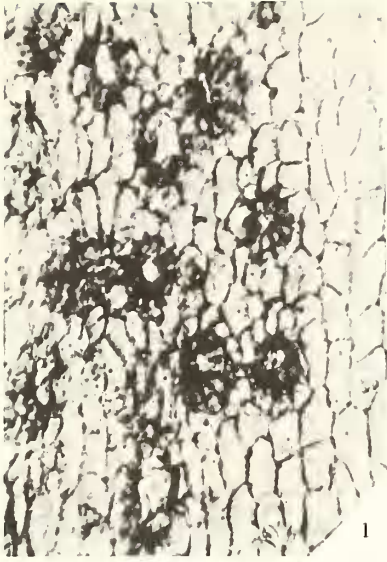
Cycadales

The concept of Cycadales is extremely confused. Originally the order was meant for megaphyllous gymnosperms in general. In this sense, the Palaeozoic pteridosperms also belong in Cycadales. In a more restricted sense, the Cycadales, comprising the two extant families Cycadaceae and Zamiaceae have little in common with any group of fossil gymnosperms. Their relations to the Mesozoic *Bjuvia-Nilssonia-Ctenis* complex remain obscure. *Cycas* from the Senonian of Sakhalin is the first undisputable Mesozoic record of this group. Thus, theories in which a putative angiosperm ancestor is modelled on *Cycas* are unacceptable, because Cycadales appeared in the geological record later than angiosperms.

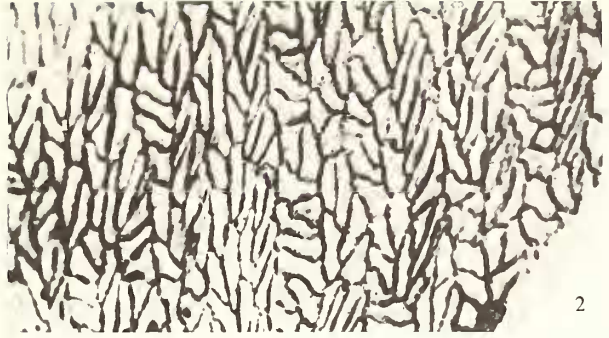
Cycas: Two pinnate leaves with single-veined pinnae from Mgachi are comparable in gross morphology with *Cycas*, *Pseudocycas*, *Paracycas*, and *Leptocycas*. However, the cuticle is characteristic of *Cycas* only. The stomata are in two bands and irregularly

EXPLANATION OF PLATE 104

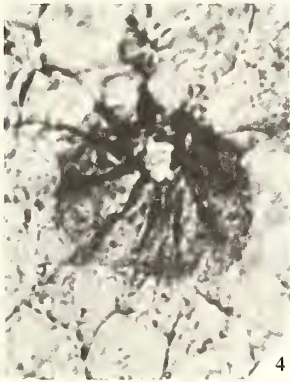
Figs. 1-7. *Cycas* from the Senonian of Sakhalin, Mgachi. 1, stomatal band, 312-290, $\times 146$. 2, alternating rows of longitudinal and transverse cells, 312-290, $\times 146$. 3, leaf, 312-290, $\times 1$. 4, stoma, external view, 312-290, $\times 395$. 5, stoma inside view showing subsidiary cells (S) and encircling cells (E) forming a chimney, SEM, $\times 1600$. 6, 7, stomata, inside view, guard cell thickenings are overlapped by the cuticle of subsidiary cells, SEM, 312-290, $\times 1600$.



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orientated. About ten encircling cells form a chimney over sunken stoma with its subsidiary cells. The guard cells are slightly above the ring of thickened subsidiary cells which extend below the guard cell thickenings overlapping about one half of their width (Pl. 104, figs. 5-7). The upper epidermis is formed by alternating bands of longitudinal, oblique, and transverse cells (Pl. 104, fig. 2). The latter feature is characteristic of the extant species *C. media*, *C. micholitzii*, and *C. thourazii*, while the stomatal structure is like that of *C. revoluta* (Pant and Nautiyal 1963). The generic assignment of the Cretaceous leaves is based on the unique combination of the gross morphology, stomatal characters, and the upper epidermis banding.

Coniferales

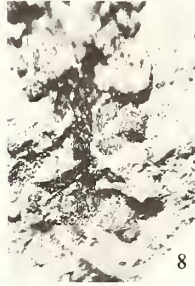
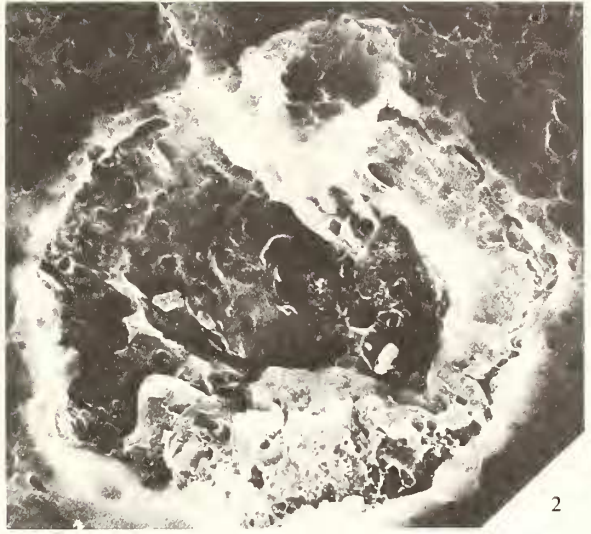
The Araucariaceae, Taxodiaceae, and Cupressaceae were major Late Cretaceous families of conifers in the Northern hemisphere. The association of *Sequoia* (or *Parataxodium*), *Cupressinocladus*, and *Protophyllocladus* occurred with amazing constancy in all localities from Greenland to Sakhalin. The Araucariaceae usually not extended beyond 50° N. (modern latitudes; the Cretaceous palaeolatitude for Mgachi is about 40° KrN.).

Araucaria: is most abundant plant in Mgachi. However, neither Heer nor Kryshtovovich mentioned it, because it is represented mostly by isolated scale-leaves which are rather inconspicuous. There are also several specimens of sparsely branching cylindrical shoots. Male strobili are in clusters, ovoid, about 6 × 4 mm. Megastrobili are globose, about 22 mm in diameter. The cone scales have a ligule and a single immersed ovule. All these characters are typical araucarian. However, the stomata are peculiar in having a peak-like outgrowth, or hair, over each stomatal pit, and each is bordered by a thickened cuticular ridge with occasional indistinct papillae. The hair is straight or hooked, with a central strand. On the inner side of the cuticle the guard cells are embraced by inward projections of subsidiary cells, while the foot of a hair forms prominent knob over them (Pl. 105, figs. 3, 4). Nothing closely comparable to this structure is known in either fossil or extant species of *Araucaria*. An obvious implication is that in the Late Cretaceous the northern araucarian stock was still diversifying and increasing the variety of its cuticular structures.

Sequoia and *Parataxodium*: No undisputed remains of *Sequoia* are known from pre-Cenomanian deposits, though some *Sequoia*-like characters have been described in such Early Cretaceous genera as *Sphenolepis* and *Athrotaxopsis*. *Sequoia* is abundant in many Late Cretaceous localities. Oswald Heer has initiated the practice

EXPLANATION OF PLATE 105

- Figs. 1-6. *Araucaria* from the Senonian of Sakhalin, Mgachi. 1, stoma, inside view, guard cells are embraced by inward extensions of the stomatal pit cuticle, 308-548, SEM, ×1100. 2, stoma, inside view, with a hair foot above, 308-548, SEM, ×1500. 3, shoot, 308-640, ×1. 4, microstrobili, 308-618, ×2. 5, abaxial cuticle of a leaf, 308-594, ×12. 6, megastrobilus, 313-264, ×1.5.
- Figs. 7-13. *Sequoia reichenbachii* (Gein.) Heer, Mgachi. 7, cone scale ('*Dammara*'), 308-599, ×3. 8, part of a microstrobilus showing microsporophylls with pollen sacs, 312-243a, ×6. 9, cone-bearing shoot with scale leaves, 307-9, ×1. 10, shoot with bifacial leaves, 307-465, ×1. 11, megastrobilus, 307-4, ×3. 12, stoma, inside view, 308-589, SEM, ×1600. 13, cells of a coastal zone, 308-589, SEM, ×1100.



of describing each shoot form under a separate name. There are 'species' with scale-leaves (*S. reichenbachii*, *S. ambigua*, *S. fastigiata*, *S. subulata*, etc.) and 'species' with linear bifacial leaves (*S. heterophylla*, *S. rigida*, *S. smittiana*, etc.). Repeated association of both forms in Greenland, European, and Siberian localities may be evidence of the leaf polymorphism characteristic of the extant species. This is confirmed also by palaeoecological observations and cuticular evidence. Epidermal cells in Senonian species are much shorter than in the extant hexaploid, suggesting diploidy or lower level of polyploidy. Microstrobili are more loose than in *S. sempervirens*. The pollen grains are poorly preserved. However, *Sequoia*-like pollen grains have been found by the author on the cuticle of *Protophyllocladus* (Pl. 106, figs. 6, 7). Judging from abundance of megafossils, *Sequoia* had a large share in the pollen rain and many pollen grains had settled on broad phylloclades of its constant associate. Some pollen grains are split as in *Taxodiaceapollenites*. Megastrobili consist of about twenty scales and many of them are preserved intact, though there are also numerous isolated scales traditionally described as '*Dammara*' or *Agathis* (Pl. 105, figs. 7, 13).

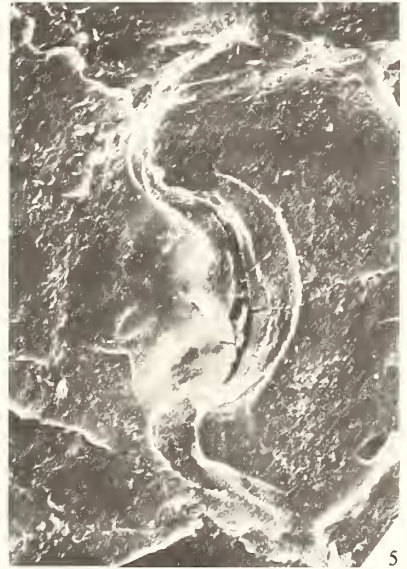
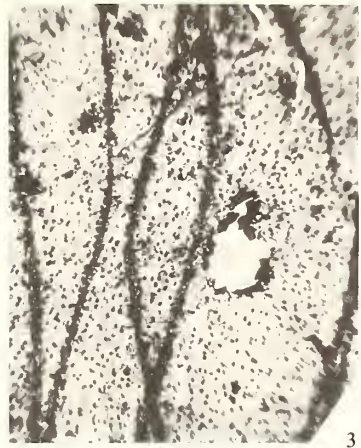
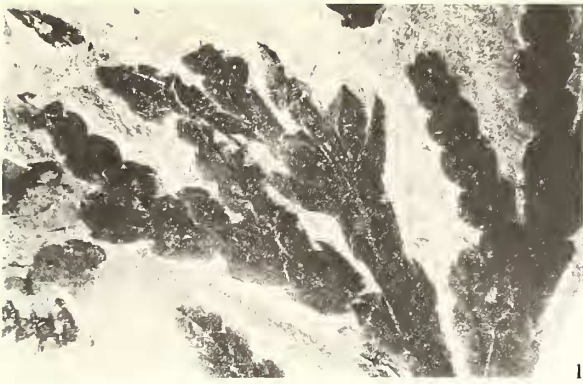
In northern Siberia and Alaska, *Sequoia* is partially replaced by a conifer with deciduous short shoots resembling those of *Metasequoia* and *Taxodium*. These shoots are often placed in *Cephalotaxopsis*, though they have little in common with the Early Cretaceous type species *C. magnifolia* Font. which belong to the Taxaceae (Florin 1958). Arnold and Lowther (1955) described extinct genus *Parataxodium* from the Late Cretaceous of Alaska. They have not compared it with '*Cephalotaxopsis*' sensu Hollick (also from Alaska), though similarity of shoots is obvious. I suggested elsewhere that numerous Siberian '*Cephalotaxopsis*' may belong to *Parataxodium*. If this was so, then *Parataxodium* was a major dominant of temperate Late Cretaceous vegetation. The Palaeocene record of *Parataxodium* from Spitzbergen is based mainly on microstrobilar characters (Schweitzer 1974). In Sakhalin, *Parataxodium* is common in the uppermost Maastrichtian localities.

At the contact of *Sequoia* and *Parataxodium* forests there was probably introgression and segregation of occasional *Metasequoia*-like and *Taxodium*- or *Glyptostrobus*-like phenotypes, such as *Glyptostrobus comoxensis* Bell which also occurred in the Senonian of Sakhalin. These genera were stabilized and achieved dominant status in the Palaeocene.

Protophyllocladus: The typical phylloclades in the Mgachi, Jonquier, and other localities are accompanied by the bipinnatifid organs which have been previously described as fern foliage. There are morphologically intermediate forms and the cuticle characters are much the same in both entire and bipinnatifid variations. Some phylloclades show minute marginal teeth. Stomata are mostly on the lower side,

EXPLANATION OF PLATE 106

- Fig. 1. *Cupressinocladus cretaceus* (Heer) Sew. from the Senonian of Sakhalin, Mgachi, branching shoot, 308-547, $\times 3$.
 Figs. 2-5. *Protophyllocladus*, same locality. 2, phylloclade showing marginal teeth, 308-612, $\times 1.5$. 3, cuticular cover with displaced veins, perforated by a fungus, showing stomata as small dots, 308-600, $\times 12$. 4, stomatal pit, 308-600, SEM, $\times 2200$. 5, guard cells, 308-600, SEM, $\times 2200$.
 Figs. 6, 7. Pollen grains, presumably of *Sequoia reichenbachii*, on the cuticle of *Protophyllocladus*, 308-600, SEM, $\times 4000$.



scattered, irregularly orientated, incomplete-amphicyclic. The stomatal pit is small, rounded, or subquadrate, bordered by a flattened cuticular ridge. Subsidiary cells are convex, without definite papillae. They differ from ordinary cells in their scabrate cuticle (Pl. 106, figs. 4, 5).

The cuticular characters suggest cupressacean rather than podocarpacean affinities. Among the Late Cretaceous Cupressaceae, *Cupressinocladus cretaceus* (Heer) Sew. resembles *Libocedrus* in hypostomatic leaves and incomplete-amphicyclic stomata. Shoots with more pronounced leaf fusion are usually placed in *Androvettia*. They display a tendency towards phylloclade formation which is more strongly manifested in *Protophyllocladus*. The author believes that *Protophyllocladus* is a member of a morphocline including also *Cupressinocladus* and *Androvettia*. Parallel development of phylloclades in Cupressaceae and Podocarpaceae can be suggested, if extant *Phyllocladus* is actually a member of Podocarpaceae. The systematic position of this genus is rather uncertain (see Keng 1963).

Thus, in the Late Cretaceous the diversity of gymnospermous orders was not reduced. Indeed, it increased due to the first appearance of the true Cycadales. The evolutionary potential of the gymnosperms were far from exhausted and they experienced important evolutionary changes. Most groups were modernized and the extant genera first appeared among Cycadales, Ginkgoales, and Taxodiaceae.

PALAEOECOLOGY

Senonian assemblages are either mono(oligo)dominant or polydominant. The first group includes:

1. *Marchantites* beds—thin siltstone layers densely covered by branching thalli.
2. Fern beds—thick siltstone layers in the upper members of deltaic cyclothems or concretion layers in turbidite facies, filled with leaves of *Anemia* and *Cladophlebis*.
3. *Nilssonia* beds—the same facies as fern beds but usually not mixed with ferns.
4. *Ginkgoites* beds—black shales and coals in alluvial and deltaic cyclothems.
5. *Sequoia* beds—lower sandy members of alluvial cyclothems and near-shore deposits with shells of marine bivalves.
6. *Quereuxia* beds—shales or silstones in alluvial cyclothems covered by floating leaf rosettes.

Gymnosperms dominate in at least three types of monodominant phytofacies which are interpreted as *Nilssonia* marshes on the margin of deltaic plains (3), pure stands of *Ginkgoites* on swampy soils (4), and allochthonous deposits of *Sequoia* (5).

The Mgachi locality is typical of the polydominant Senonian assemblages. The numerical representation of species in this locality is as follows (bryophytes omitted):

	Number of specimens	%		Number of specimens	%
<i>Sequoia</i>	605	34.7	<i>Protophyllum</i>	42	2.4
<i>Araucaria</i>	308	17.7	<i>Nilssonia</i>	31	1.8
<i>Protophyllocladus</i>	269	15.5	<i>Ginkgoites</i>	25	1.5
<i>Araliaephyllum</i>	127	7.2	<i>Sagenopteris</i>	20	1.2
<i>Cupressinocladus</i>	87	4.9	<i>Cyathea</i>	14	0.8
<i>Trochodendroides</i>	77	4.4	<i>Liriophyllum</i>	2	0.1
<i>Debeya</i>	60	3.5	<i>Magnoliaephyllum</i>	2	0.1
<i>Anemia</i>	32	2.8			
<i>Cladophlebis</i>	40	2.4	Total	1741	100

To distinguish between the local and regional dominants, the importance value (IV) was calculated as

$$\frac{100p_1}{M} + \frac{100d_1}{M}$$

(p_1 —number of localities in which a species is present, d_1 —number of localities in which it is dominant, M —total number of localities).

For the most important species IV is ($M = 28$):

	d	d	IV		d	d	IV
<i>Sequoia</i>	25	18	153.42	<i>Nilssonina</i> (2)	8	2	35.7
<i>Protophyllocladus</i>	17	6	82.13	<i>Myricaephyllum</i>	8	1	32.14
<i>Ginkgoites</i>	14	4	64.28	<i>Araliaephyllum</i>	6	1	24.99
<i>Protophyllum</i>	13	5	64.22	<i>Debeya</i> (1)	4	2	21.41
<i>Nilssonina</i> (1)	13	4	60.7	<i>Araucaria</i>	3	2	17.85
<i>Cupressinocladus</i>	13	4	60.7	<i>Parataxodium</i>	3	2	17.85
<i>Trochodendroides</i>	11	4	53.54	<i>Liriophyllum</i>	3	1	14.28
<i>Magnoliaephyllum</i>	8	3	39.28	<i>Debeya</i> (2)	2	1	10.71

The resultant picture is that of *Sequoia* forest with *Protophylocladus* and *Cupressinocladus* as major subdominants. *Araucaria* is a local dominant in Mgachi. In respect to the dominant angiosperm morphotypes, there were two aspects of redwood forest: *Sequoia*-laurophyllous with *Laurophyllum*, *Magnoliaephyllum*, and *Araliaephyllum* (see Krassilov 1973) and *Sequoia*-platanophyllous with *Protophyllum*. The general composition of *Sequoia* forest remained unchanged through the Senonian, though relative abundance of the angiosperm morphotypes varied from a few laurophylls in the Coniacian to their preponderance in the Campanian followed by a sharp decline in the Maastrichtian.

In the Boshniakovian Formation, only two types of assemblages are recognized: fern beds, fine-grained tuffites with *Woodwardia* and *Cladophlebis*, and *Metasequoia*-*Corylites* beds, tuffaceous rocks with polydominant assemblage including *Alnites*, *Platanus*, and *Liriophyllum* as major subdominants.

THE TERMINAL CRETACEOUS EVENT

There is an abrupt floristic change between the late Maastrichtian (paralic beds with *Sequoia*, *Parataxodium*, and *Nilssonina*) and Danian (tuffaceous Boshniakovian beds with *Metasequoia*, *Corylites*, and *Alnites*). In the transitional beds (about 1.5–2 m), *Pterophyllum* and *Trochodendroides* associate with *Glyptostrobus* and *Alnites*. The major events are:

Extinction of the Caytoniales and Bennettitales, sharp decline of Nilssoniales and Ginkgoales, followed soon by extinction of *Nilssonina* in the Danian. The Cretaceous terminal extinction was not preceded by a gradual decline. In Mgachi, *Sagenopteris* with numerical representation of 1.2% ranks among common species, inferior only to *Araliaephyllum polevoi* among angiosperms. In fact, it is more abundant here than in any Jurassic locality. In the latest Maastrichtian, *Ginkgoites* beds are common and *Nilssonina* beds are more frequent than in the underlying strata. These phytofacies vanished at the Maastrichtian–Danian (K–T) boundary. About 50 my of coexistence with angiosperms scarcely affected the ecological status of *Sagenopteris* and *Nilssonina*. It is highly improbable that their extinction was caused by competitive exclusion.

Replacement of dominant types of conifers; *Sequoia*, *Parataxodium*, *Cupressinocladus*, and *Protophylocladus* which formed a core of the Late Cretaceous assemblages,

were succeeded by *Metasequoia-Taxodium-Glyptostrobus* complex. *Protophyllocladus* perished together with Cretaceous species of *Sequoia* and *Cupressinocladus*.

Replacement of dominant leaf morphotypes among angiosperms; *Araliaephyllum*, *Protophyllum*, and *Debeya* gave way to *Corylites* and *Alnites*. Such morphotypes as *Trochodendroides*, *Menispermites*, and *Magnoliaephyllum* transgressed the boundary, but their species content changed. On the species level, only *Liriophyllum sachalinense* Krysh. survived the Cretaceous-Tertiary extinction in Sakhalin, though there were some morphological differences between Senonian and Danian leaf populations.

Phytocenological changes were even more spectacular than the taxonomical. Dominant Cretaceous communities—*Sequoia*-laurophyllous forests—died out and were replaced by mixed broad-leaved forests. This change was even more important for the world ecosystems than the extinction of the dinosaurs.

One can wonder how to reconcile these statements with assertions of other palaeobotanists that nothing particular happened at the Cretaceous-Tertiary boundary. According to Hickey (1977), 95% of genera crossed the boundary. Jarzen (1977) has not found drastic changes in the palynological record. Both authors have dealt with angiosperms only. The identifications of Cretaceous angiosperm leaves with extant genera are mostly in error and the organ-genera based on leaf remains are morphotypes lumping unrelated species. Many morphotypes have survived from the Albian to the present. This fact is of little evolutionary importance, though the proportions of different morphotypes in a flora have some ecological meaning. The same can be said of the pollen morphotypes. Jarzen admitted that the proportion of animal- versus wind-adapted pollen types changed at the Cretaceous-Tertiary boundary. This may reflect important changes of vegetation and climate. He relied on unpublished work of Tschudy in stating that the differences between Cretaceous and Tertiary palynofloras become less and less with the progress of studies. However, in his published work Tschudy (1977) recognized a sharp decline of the dominant Cretaceous pollen types *Normapolles* and *Triprojectacites* at the Cretaceous-Tertiary boundary. Though these pollen morphotypes survived up to the Eocene, their numerical representation and species content changed dramatically within the Cretaceous-Tertiary stratocotone.

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